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Factors affecting duration of the postcapping period in brood of the honey bee (*Apis mellifera carnica*)

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SUMMARY

Reducing the duration of the length of the capped brood phase is considered to be a good approach for breeding honey bees resistant to *Varroa jacobsoni*. In cross-fostering experiments using six colonies of *Apis mellifera carnica*, in addition to the genotype of worker brood, the nursing colony also affected the duration of the postcapping stage. Regression analysis of postcapping duration on precapping duration showed that the relationship was negative and highly significant ($b = -0.05$, $P < 0.001$), so that a shorter postcapping stage was partly compensated for by a longer precapping period. The ratio between postcapping and precapping periods was significantly affected by genotype of worker brood ($P < 0.001$), by effects of the precapping nurse colony ($P = 0.008$) and by effects of the postcapping nurse colony ($P < 0.001$). The duration of the precapping and postcapping stages and the inverse relationship between them was shown to have a genetic basis. The results show that the nurse colony has an important impact on the duration of the postcapping stage and this should be considered in selection programmes.

Keywords: *Varroa jacobsoni*, honey bee brood, *Apis mellifera carnica*, development, postcapping period, genotype, resistance, honey bee colonies, brood rearing, inheritance, selection

INTRODUCTION

The honey bee ectoparasite *Varroa jacobsoni* reproduces only in capped brood cells. As hypothesized by Moritz and Hänel (1984) and found by Büchler and Drescher (1990), the shorter the postcapping stage of honey bee brood the fewer offspring *V. jacobsoni* females are able to produce. Therefore the duration of the postcapping stage is assumed to be an important factor for breeding bees resistant to *V. jacobsoni* (Moritz, 1985; Schousboe, 1986; Büchler & Drescher, 1990; Jordan, 1991; Moritz & Jordan, 1992; Harbo, 1992). Heritabilities of postcapping duration are quite high (Moritz, 1985; Büchler & Drescher, 1990; Jordan, 1991; Moritz & Jordan, 1992; Harbo, 1992; Le Conte *et al.*, 1994), so the response to selection is expected to be sufficient. But regulation of development time in the honey bee is governed by several components, including the genotype of the worker larvae and the nurse colony in which the brood is reared (Rosenkranz & Engels, 1994). The relative importance of these factors should be considered when designing performance tests and breeding programmes.

It is likely that the duration of development is optimized by natural selection. Selection for a shorter development may hinder the expression of other traits. Lints and Lints (1970) observed in *Drosophila* an unfavourable relationship between the speed of development and the characteristics of the adult. Bienefeld (1993) did not find a significant relationship between some morphological characters and developmental speed in unselected queen honey bees. The honey bee may profit from the fact that total development is composed of two stages, which have quite different bearings on the reproduction of *V. jacobsoni*. Because the mite cannot utilize the precapping stage of the host for reproduction, the partitioning of the two developmental stages is worthy of attention. Bienefeld (1993) found a negative relationship between the length of the precapping and postcapping period in queen honey bees giving the advantageous result that a shorter postcapping stage may be partly compensated for by a longer precapping period. The overall development was only slightly affected by a shorter postcapping stage duration. It was uncertain whether there was a genetic basis for the inverse relationship between precapping and postcapping stage duration, or which factors influenced any such correlation. I examined the nature of this relationship and the influence of the colony which nursed the brood before capping and after capping.

MATERIALS AND METHODS

Six strong colonies of *Apis mellifera carnica* of different descent (queens from Hungaria and Chechia, three queens from German breeding lines and a free-mated queen) were used in this study. The colonies were held in polystyrene hives. During the time of monitoring egg laying, the queens were confined to a single brood comb. The time of egg laying was determined by marking individual cells on a plastic sheet at 2-h intervals. In the evening, brood combs with freshly laid eggs were divided into thirds. One piece was returned to the brood nest of the colony from which it originated, and the others were distributed among two of the other five colonies. Shortly after cell capping, which was also monitored at 2-h intervals, the capped brood pieces were again divided into smaller pieces. Again, one brood piece stayed in its own colony while the others were distributed among the other colonies. Twenty-four hours before emerging the brood pieces were placed in an incubator (34.50°C, 50–60% RH). In order to determine the time of emergence, an infra-red barrier system was set up. A transmitter (GL 480, Sharp Corp., Osaka, Japan) and receiver unit (Sharp IS 471F) were fixed to small cages, which were attached to each single cell to be monitored (fig. 1). When emerging, the bees interrupted the infra-red light beam and the time of emergence was thereby measured and recorded on a personal computer. Between 2 May and 15 June this experiment was carried out eight times. Each of the eight environmental subgroups consisted of two sets, and the procedure for each group was carried out on two successive days.

The following statistical model was used to partition the sources of variance:

$$y = s + g + n_1 + n_2 + e$$

where:

y = observed duration of development or ratio between postcapping and precapping stage duration;

s = effect of environmental subgroups (4 levels);

g = effect of the genotype of the brood (6 levels);

n_1 = effect of precapping nurse colony (6 levels);

n_2 = effect of postcapping nurse colony (6 levels);

e = error.

Variance components for effects of subgroup, genotype of worker brood, precapping nurse colony and postcapping nurse colony were estimated by the restricted maximum likelihood method (SAS, 1988). The relative importance of these effects was given by the ratio of the corresponding variance component and the total variance ($s_s^2 + s_g^2 + s_{n1}^2 + s_{n2}^2 + s_e^2$). The least-squares means, which are the expected values of class means for a balanced design adjusted for the other influencing factors, were also computed by an SAS (1988) routine.

RESULTS

Total development of worker bees took 483 h 24 min ± 13 h 12 min ($\bar{x}$ ± s.d.), made up of a 191 h 54 min ± 5 h 18 min long precapping period and a 291 h 30 min ± 12 h 48 min long postcapping period (n = 779).

Precapping, postcapping and total developmental durations were affected by the genotype of worker brood (table 1). The relative importance of the genotype, as

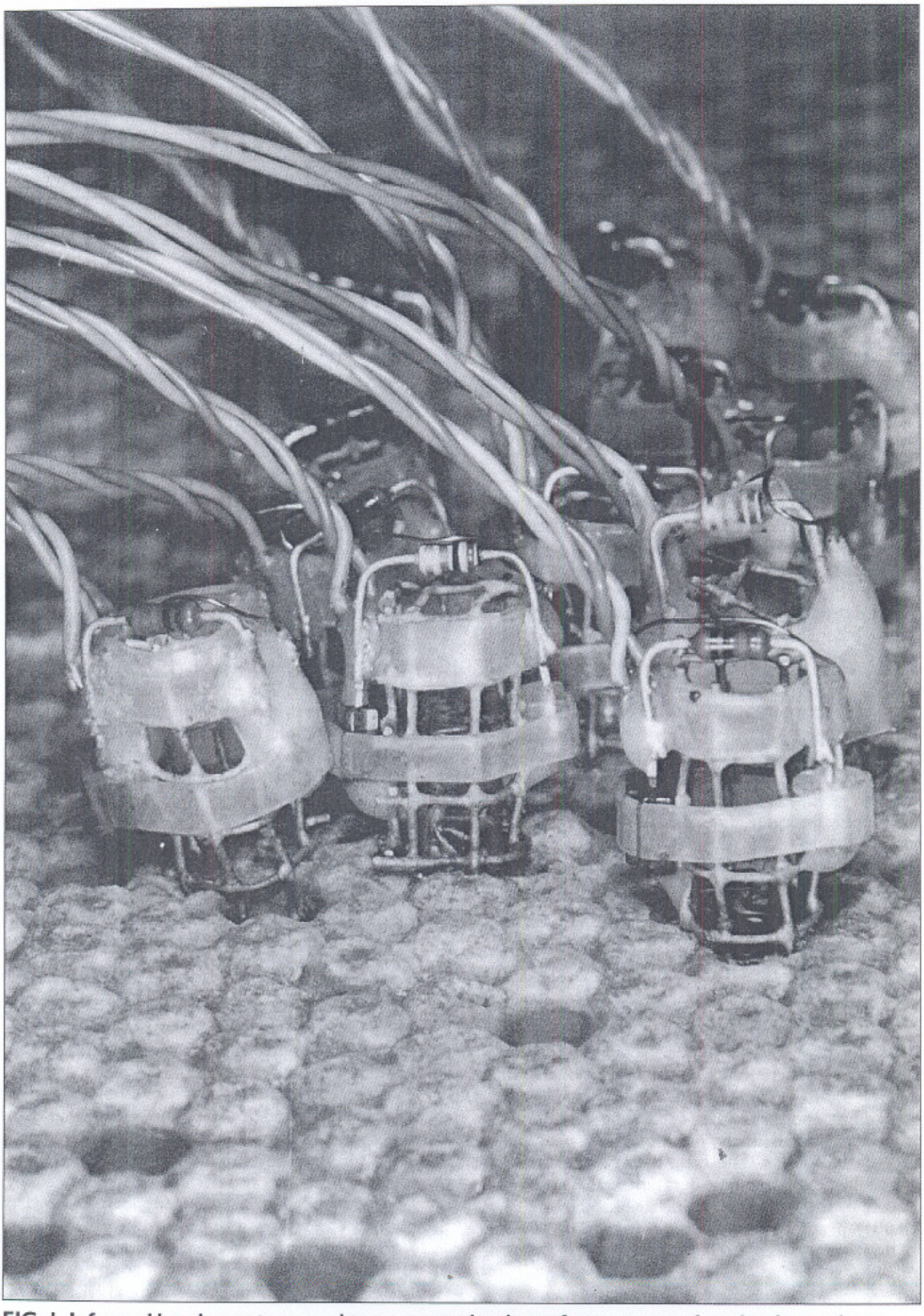

FIG. 1. Infra-red barrier system used to measure the time of emergence of worker honey bees.

TABLE 1. Analysis of variance and variance components for different developmental stages of worker honey bees.

Source of variance	Anova (F values) Developmental stage			Variance components (%) Developmental stage		
	precapping	postcapping	total development	precapping	postcapping	total development
Genotype of worker brood	10.4[2]	12.7[2]	7.1[2]	5.4	13.5	7.6
Precapping nurse colony	16.9[2]	0.7[ns]	0.7[ns]	12.0	0.0	0.0
Postcapping nurse colony	–	7.8[2]	5.5[2]	–	6.9	4.9
Environment	79.8[2]	6.4[2]	2.7[1]	40.0	2.8	2.7

[1]P = < 0.05
[2]P = < 0.001
[ns]Not significant

shown by variance components estimates, was 5.4% for precapping duration, 13.5% for postcapping duration and 7.6% for total development duration. Least-square means for these effects for the six colonies are given in figure 2. For example, the least-square means for genotype indicate the average effect of the genotype of a colony, independent of the precapping or postcapping nurse colony used.

The precapping nurse colony influenced the duration of the precapping period ($F = 16.9$, $P < 0.001$), whereas postcapping ($F = 0.7$, $P > 0.05$) and total development duration ($F = 0.7$, $P > 0.05$) were not affected by the source of precapping larval care (table 1). After capping, the nurse colony significantly influenced duration of the postcapping period ($F = 7.8$, $P < 0.001$) and total development period ($F = 5.5$, $P < 0.001$). With nearly 7% of the variance (table 1), this factor is quite important in regulating postcapping stage duration. Variation among environmental subgroups very strongly influenced duration of the precapping stage ($F = 79.8$, $P < 0.001$). However, the duration of the postcapping stage ($F = 6.4$, $P < 0.001$) and of the total development ($F = 2.7$, $P < 0.05$) were also significantly affected by environmental subgroup effects.

Regression of postcapping duration on precapping duration showed a significantly negative relationship ($b = -0.05$, $F = 12.5$, $P < 0.001$) between these variables. Accordingly, shortening the postcapping stage duration by one unit increases the duration of the precapping stage by 0.05 units. The ratio between postcapping duration and precapping duration was significantly affected by the genotype of worker brood ($F = 20.4$, $P < 0.001$), precapping nurse colony ($F = 3.3$, $P = 0.008$), postcapping nurse colony ($F = 10.0$, $P < 0.001$) and enviromental subgroup ($F = 28.2$, $P < 0.001$). The least-squares means for this ratio are given in figure 3. The relative importance of these factors, given by variance component estimates, was found to be 16.1% for genotype (giving a 'heritability' of 0.51), 3.1% for precapping colony, 9.0% for postcapping colony and 14.7% for environmental subclass.

DISCUSSION

Confirming the results of Harbo (1992), total development at 20 days 3 h was much shorter than generally accepted. Moreover, in other experiments under different climatic conditions (unpublished results) the development time of worker honey bees very rarely exceeds the normal development time of 21 days.

Phenotypic variation in development time differed between the developmental stages, although it was relatively small at all stages. The coefficient of variation for postcapping stage duration (4.4%) was nearly twice as large as for precapping stage duration (2.7%), or duration of total development (2.7%). Durations of all development periods were significantly affected by the genotype of worker brood being reared. Using the corresponding variance components in table 1, h^2 had values of 0.17 for precapping stage, 0.43 for postcapping stage and 0.24 for total development. However, the number of colonies involved was too small to get realistic estimates of the heritability. Nonetheless, Harbo's (1992) estimate for the heritability for the duration of the postcapping period ($h^2 = 0.61$) was also higher than his corresponding values for the uncapped period ($h^2 = 0.41$) and for total development ($h^2 = 0.52$). Consequently, selection response per generation, depending on the product of heritability (h^2), phenotypic standard deviation (s_p) and intensity of selection (i) (Falconer, 1981) is expected to be highest in the postcapping period. Moritz (1985) assumed selection response for a shorter postcapping stage duration in *A. m. carnica* to be very small, due to the small standard deviation.

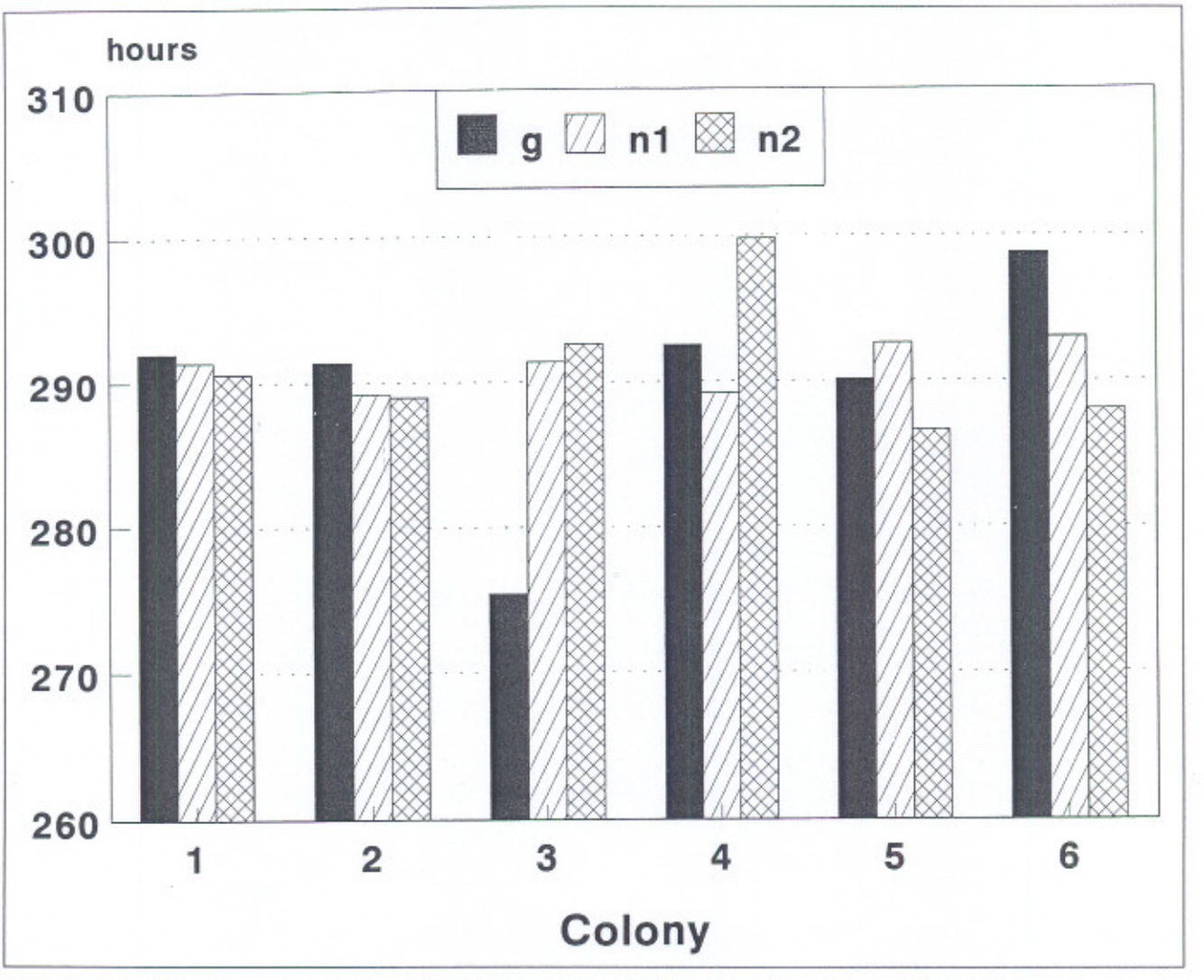

FIG. 2. Effect (least-squares means) of the genotype (g), precapping nurse colony (n_1), and postcapping nurse colony (n_2) of six colonies on postcapping stage duration.

However, using the results of the studies of Harbo (1992) and Le Conte *et al.* (1994), selection response per year can be expected to be between 1.5% and 2% with respect to the population mean. These estimates, which were derived from somewhat simplified assumptions (mass selection, selection in both sexes, same intensity of selection (p = 20%), and a generation interval of one year in both sexes), coincide with findings in traits for other agricultural species (Bienefeld, 1990).

In contrast to the results of Le Conte *et al.* (1994), a significant nurse colony effect was observed. Le Conte *et al.* placed the brood in an incubator after capping, and thus measured only the effect of the precapping nurse colony; the effect on the duration of the postcapping stage was found to be negligible. Moritz (1985), however, measured a significant effect of the precapping nurse colony after also having moved brood to an incubator after capping. The different results may have been due to different honey bee races being used in the two studies. The precapping nurse colony may, and the postcapping nurse colony does, influence the duration of the postcapping stage. Spivak *et al.* (1990) showed temperature to be significant for speed of development in queen honey bees. The thermoregulation of a colony is assumed to be the most important factor of the postcapping nurse colony effect, and was shown by Nuñez (1979) and Rosenkranz and Engels (1994) to be partly genetically determined. In breeding programmes designed to shorten the postcapping duration (e.g. Harbo, 1992; Wilde & Koeniger, 1992), where the worker brood is transferred to an incubator or the performance test is run in mating boxes, the effect of the nursing ability of colonies on this trait is not measured. As a result it is not possible to quantify the overall postcapping nursing ability of a colony by testing the duration of the postcapping stage in other situations, but with full colonies during the whole period. Selection both for faster development of the brood and for nursing ability to speed development will improve genetic gain by shortening the duration of the postcapping stage. The testing procedure for duration of the postcapping stage may be modified so that the brood is kept in the colony from which it originated as long as possible in order to measure also the genotype for nursing ability. This may be especially important, because different

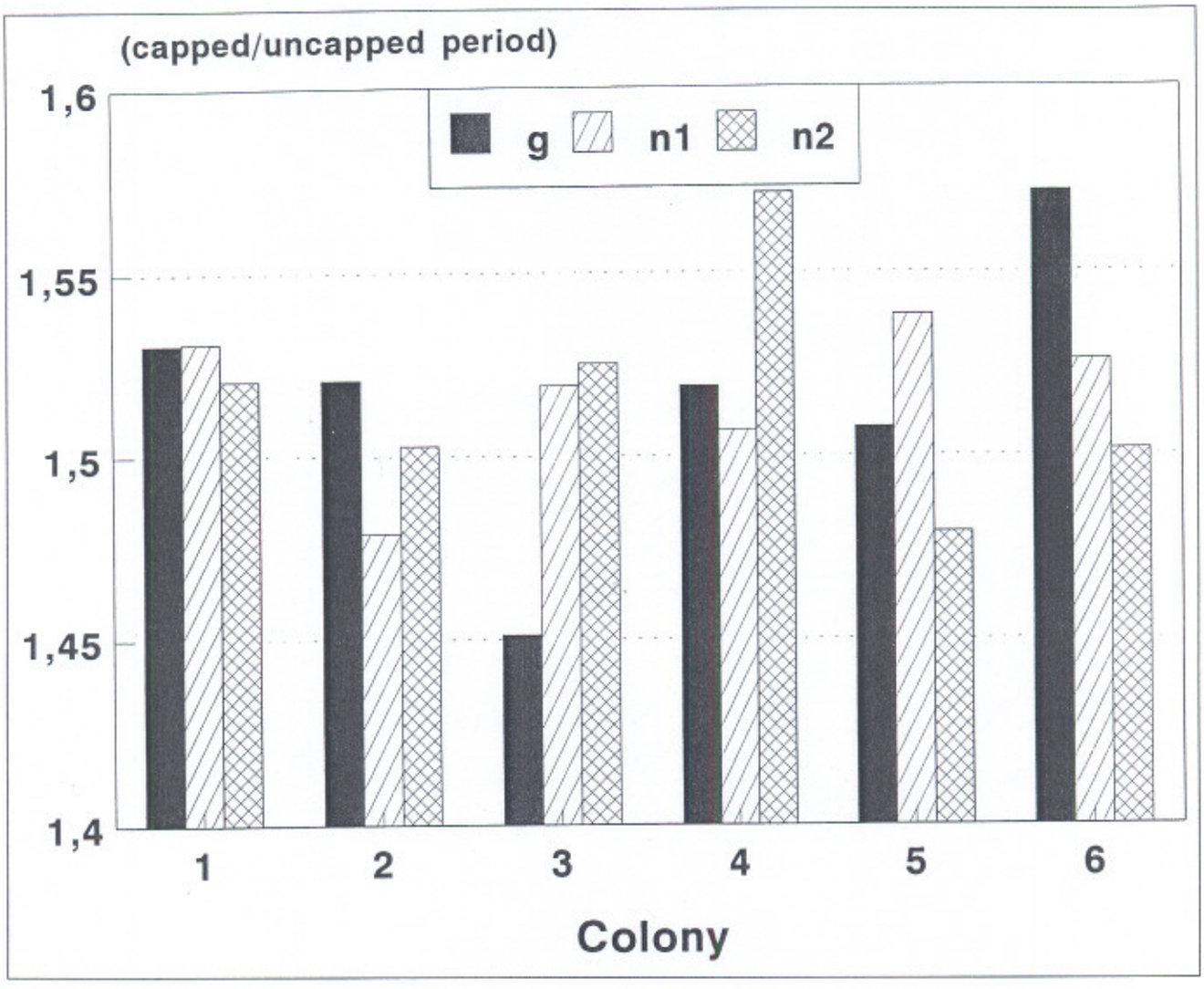

FIG. 3. Effect (least-squares means) of the genotype (g), precapping nurse colony (n_1), and postcapping nurse colony (n_2) of six colonies on the ratio between the duration of postcapping and precapping stage.

least-squares means for the three effects on the duration of the postcapping stage within the colonies indicate that superiority for one effect does not necessarily indicate superiority for other effects. The more the nursing colony effect is inherited, the more beneficial efforts in testing full colonies will be.

As demonstrated for queen honey bees (Bienefeld, 1993), a shorter postcapping stage in workers, is partly compensated for by a longer precapping stage. In addition to the influences of the nurse colony on the relationship between the duration of the precapping and postcapping stages, a significant genetic effect on this inverse ratio was also found. This may raise hopes of selecting strains of honey bees with a shorter postcapping period (thereby hindering reproduction of *V. jacobsoni*), but with a longer precapping period. However, due to the significantly larger contribution of the duration of the postcapping stage (60%) to the total development time and the relatively small coefficient of regression, selection for a shorter postcapping stage is only partially offset by the extended duration of the precapping stage. Further investigation is needed in order to determine whether speed of development correlates with important traits in the honey bee.

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